

Searching for a Life History Approach to Salmon Escapement Management

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Abstract.—A number of Pacific salmon populations have already been lost and many others throughout the range are in various states of decline. Recent research has documented that Pacific salmon carcasses serve as a key delivery vector of marine-derived nutrients into the freshwater portions of their ecosystems. This nutrient supply plays a critical biological feedback role in salmon sustainability by supporting juvenile salmon production. We first demonstrate how nutrient feedback potential to juvenile production may be unaccounted for in spawner-recruit models of populations under long-term exploitation. We then present a heuristic, life history-based, spreadsheet survival model that incorporates salmon carcass-driven nutrient feedback to the freshwater components of the salmon ecosystem. The productivity of a hypothetical coho salmon population was simulated using rates from the literature for survival from spawner to egg, egg to fry, fry to smolt, and smolt to adult. The effects of climate variation and nutrient feedback on survival were incorporated, as were density-dependent effects of the numbers of spawners and fry on freshwater survival of eggs and juveniles. The unexploited equilibrium population was subjected to 100 years of 20, 40, 60, and 80% harvest. Each harvest scenario greater than 20% brought the population to a reduced steady state, regardless of generous compensatory survival at low population sizes. Increasing harvest reduced the positive effects of nutrient contributions to population growth. Salmon researchers should further explore this modeling approach for establishing escapement goals. Given the importance of nutrient feedback, managers should strive for generous escapements that support nutrient rebuilding, as well as egg deposition, to ensure strong future salmon production.

Introduction

No longer is it news that Pacific salmon *Oncorhynchus* spp. populations are declining and, in some cases, disappearing. The critical questions now are whether, and to what extent, the Pacific Northwest populations can recover and whether apparently healthy populations in Alaska and British Columbia can be protected from further declines. Much of this book focuses on the science of nutrient cycling in freshwater ecosystems. There are clear ecological links between salmon carcass-derived nutrients and aquatic ecosystem

health including subsequent salmon production (e.g., Kline et al. 1990; Bilby et al. 1996; Cederholm et al. 1999). Although awareness of a nutrient deficit in freshwater ecosystems is rapidly growing (e.g. Gresh et al. 2000; Stockner et al. 2000), there are few quantified relationships between the biomass of spawners entering aquatic habitats and resultant future run sizes (Bilby et al. 2001). This chapter evaluates a new paradigm wherein salmon escapement management includes life history-based production limits and nutrient feedback.

Reduced nutrients in the freshwater ecosystem, due to diminished spawning escapements,

is just one of many causes interacting to deplete salmon runs. While a salmon population may sometimes decline due to an obvious cause, such as overfishing, dams, or loss of estuarine intertidal habitats to development, in most cases, the decline is attributable to a complex, negative synergism of anthropogenic and natural assaults (see NRC 1996, Stouder et al. 1997; Knudsen et al. 2000). Although sorting out the role of reduced nutrients from other harmful factors may be impossible, the topic warrants specific attention. The relative importance of nutrient cycles in the southern part of the Pacific salmon range is obscured by habitat alteration. However, there are a number of relatively pristine watersheds that have limited runs. If the science on nutrient cycling is correct, lack of salmon in these apparently healthy stream systems may indicate that overfishing has been the primary cause of run reduction. In the northern portion of the range, where many habitats are intact, the effects of potential reductions in nutrients may be more difficult to detect but could be contributing to recent declines in some areas.

The enormous scientific attention focused on Pacific salmon management practices over the years makes the pervasive population declines difficult to reconcile and accept. Existing management practices clearly lack some important elements. The primary weakness is likely the absence of an integrated approach that accounts for all the major factors impinging on salmon populations throughout their ecosystem (Lichatowich et al. 1995; Mobrand et al. 1997), including nutrient cycling (Williams et al. 1999). Nutrient cycling has been alluded to in several previous reconsiderations of carrying capacity and salmonid ecosystems (Spence et al. 1996; Mobrand et al. 1997; Williams et al. 1999). While these new studies set the stage for fully integrating nutrient cycles into management modeling, they have only considered nutrients in a limited contemporary context, rather than striving to assess the full biological capacity of aquatic ecosystems when optimally fertilized by salmon carcasses. Therefore, this chapter will 1) reinforce why previous approaches to salmon escapement management have been less than successful, 2) propose a new way of thinking about escapement management that accounts for critical life history characteristics and nutrient feedback loops, and 3) make research and management recommendations that support salmon biological productivity.

True Salmonid Carrying Capacity

A central unknown in salmon population dynamics is the *true* carrying capacity. Some have referred to this concept as “pristine carrying capacity.” We use the term “true carrying capacity” to acknowledge that many populations may never return to the pristine conditions that occurred prior to non-indigenous human settlement. However, even in altered habitats, salmon populations have an intrinsic capacity for colonization and rebuilding (e.g., Milner et al. 2001) that should be maximized. Regardless of the habitat condition, the challenge is to understand how many salmon a given population can sustainably produce (Mobrand et al. 1997).

The spawner-recruit model (e.g., Ricker 1975) adequately describes the number of offspring produced from a given number of spawners if all the assumptions are met; however, such models often incorrectly estimate escapement at maximum sustainable yield (MSY) and results in an inappropriate harvest rate (Hilborn and Walters 1992; Needle, in press). This can result from measurement error, time series bias due to lack of independence, and nonstationarity of the spawner-recruit relationship (Hilborn and Walters 1992).

The spawner-recruit model can also underestimate the true production capacity and, particularly, the unexploited equilibrium replacement point in an exploited population (Knudsen 2000, in press). When the model is fit to contemporary data, there is rarely any information to judge the assumption that the population is currently performing at full production potential. For example, recent core analyses of historic marine-derived nitrogen in Alaskan sockeye lakes demonstrate that some populations in unaltered habitats are producing less salmon than they did before heavy exploitation (Schmidt et al. 1998; Finney et al. 2000). These data provide a rare surrogate for historic, pristine escapement that can be compared to contemporary escapements. We mimicked these concepts and generated hypothetical run size data for a generic salmon population before and after exploitation (Figure 1, top panel). Extended exploitation reduces both the number of spawners at MSY estimated by the spawner-recruit model, relative to the system's potential (Figure 1, middle panel), and the equilibrium replacement point, which is drastically

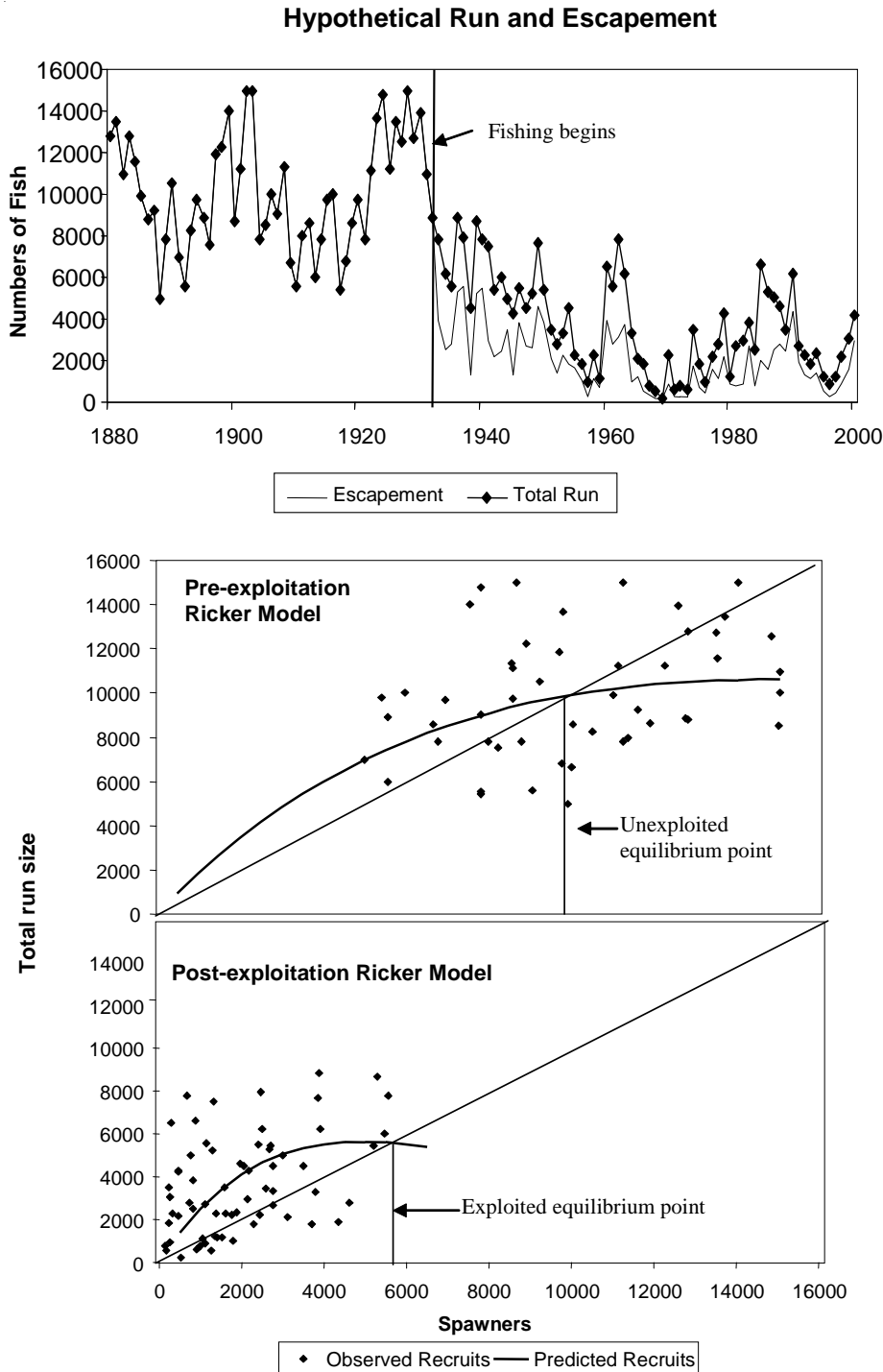


FIGURE 1. Hypothetical coho salmon population total run size before exploitation and total run and escapement after exploitation (top panel). Ricker spawner-recruit plots of the pre-exploitation data (middle panel) and post-exploitation data (bottom panel) from the same habitat. Note that the equilibrium population replacement point has shifted to dramatically fewer spawners under exploitation even though the habitat has not changed.

reduced under exploitation (Figure 1, bottom panel). If the system were performing to its full biological capacity, the exploited equilibrium point would be the same as in the unexploited state. Any harvested production that is truly “excess” should not reduce the ability of the population to replace itself at its full production capacity.

The effectiveness of spawner-recruit models is further compromised by the inconsistencies and dynamics of the real world. The spawner-recruit model is a composite of all the factors that influence salmon production, “averaging” all historic observations into one relationship. Yet those factors are highly variable from year to year, and the limiting factors can change annually. Because of the drawbacks to salmon spawner-recruit modeling, a new model accounting for the multiple and variable limitations to survival, including nutrient cycling, will be required for successful future management. Admittedly, application of such an analytical system to salmon management is a long way off, but we encourage thought in that direction and offer the following preliminary model as a step in the right direction.

A Proposed Life History Approach to Escapement Management

Life history approaches to managing Pacific salmon have been proposed previously (e.g., Lichatowich et al. 1995; Mobrand et al. 1997; Nickelson and Lawson 1998). Nickelson (1998) and Bradford et al. (2000) estimated escapement needs by focusing on life-history and habitat-oriented modeling, but they assessed capacity using recent observations (i.e., from populations normally exploited) and did not explicitly include nutrients in their models. Our approach is based on a stepwise accounting of mortality throughout the salmon's life, attempting to account for all major mortality sources, as generally illustrated in Figure 2.

The new approach was evaluated using a heuristic spreadsheet model to simulate the life history of a simplified coho salmon *O. kisutch* population (coho were selected because they mostly return at the same age and they depend on nutrients during freshwater rearing). We estimated relationships at each life history step and

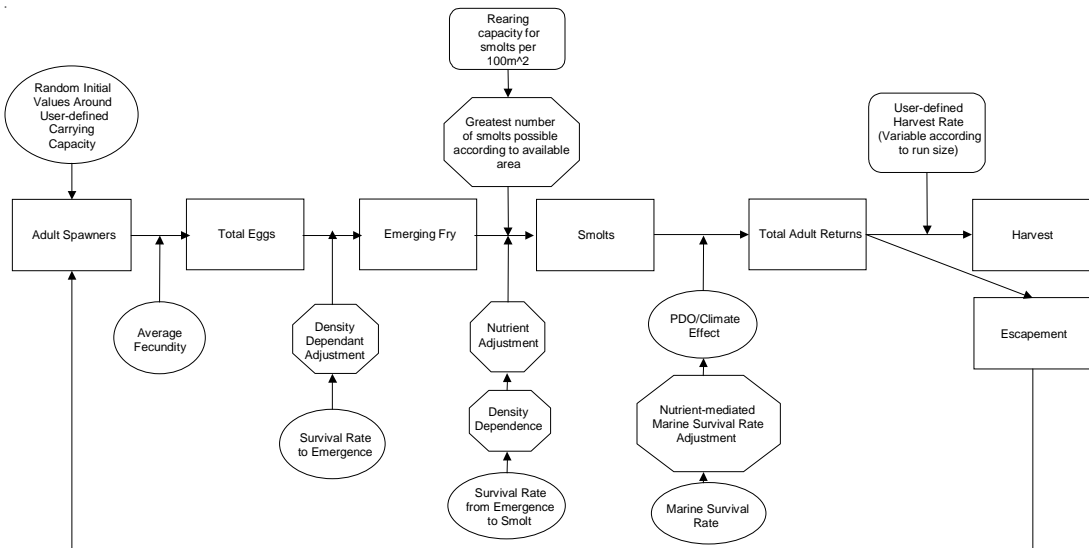


FIGURE 2. Flow chart illustrating the modeled coho salmon life cycle. Rectangles indicate life history stages where population numbers are calculated. Ovals represent stochastically varied user inputs. Rounded rectangles include user inputs that are not directly stochastically varied. Octagons are stochastically varied density-dependent survival adjustments.

included nutrient and density dependent feedback, as well as appropriate stochasticity, where relevant. Ideally, the model would be parameterized based on empirical observations for any population of interest. However, our first generation model is based on a hypothetical coho salmon population for which we assume we know the appropriate parameters (not the same data illustrated in Figure 1). We estimated mortality rates and their variation, based on informal meta-analysis from the literature or educated guesses of reasonable values based on coho salmon ecology.

A key feature of this preliminary investigation is the assertion that we know the true population equilibrium replacement point. If a population was not exploited and did not experience major perturbations or long-term climatic trends, it would exhibit interannual escapements always varying around the true equilibrium replacement point (for example, see Figure 1, middle panel). A predefined, unexploited equilibrium point is our standard reference point for assessing population performance under various scenarios of nutrient feedback and harvest rate.

Compensatory survival following exploitation is accounted for in the model by increasing intragravel survival and freshwater rearing survival when spawner densities are less than the equilibrium number of spawners. Incubation and rearing survivals were likewise reduced when spawners or fry were above average. When spawners were above the unexploited equilibrium, we included positive nutrient-derived adjustments to rearing survival (Quinn and Peterson 1996) and marine survival (Bilby et al. 1998) because of larger smolt size resulting from improved food production.

Model Assumptions

Our coho salmon life history model functions under several important assumptions.

- The population equilibrium replacement carrying capacity is known.
- The population does not experience catastrophic perturbations lasting more than one generation.
- There is no nutrient effect from other salmon species.
- The nutrient effect comes only from the parental escapement.
- There is no freshwater or marine competition with other runs or species.
- The male:female ratio is 1:1.
- There is no effect from jacks.
- Natural mortality between harvest and spawning is negligible.
- There is neither a genetically based deleterious effect at small population size nor compensatory genetic effects for extremely small populations.
- Fish do not stray from or into the population.

Model Steps

Each row in the spreadsheet represents one annual cohort. Survival rates and associated variations for each life history stage are computed in the columns. The escapement resulting at the last step (column) in the model feeds the number of spawners for the beginning of the resulting cohort three years (rows) later. There are 100 annual cohorts in the model. The model begins deterministically in that sex ratio, fecundity, egg to fry survival, fry to smolt survival, and marine survival balance to the original number of spawners in the unexploited state. Survival rates are stochastically modified based on variations reported in the literature. Carcass-derived nutrient feedback and marine environmental variation simulations further modified survival but only to the extent that the unexploited population remained approximately balanced over model iterations.

The model allows the user to input certain values for the population of interest: equilibrium carrying capacity (number of spawners), stream area (m^2), maximum smolt production (per 100m^2), the maximum expected fry to smolt survival rate (used only to calculate a reference point for fry density dependence), and the intended harvest rate (Figure 2). At the start of each model run, the initial spawners for years 1, 2, and 3 were generated randomly using a normal distribution with a mean of the user-input equilibrium spawner carrying capacity and a standard deviation of 10%.

Fecundity values were randomly generated using a normal distribution with a mean of 4,500 eggs (Groot and Margolis 1991) and standard deviation of 500. Assuming a spawner sex ratio of 1:1, the total potential number of eggs was equal to the number of spawners divided by 2 and multiplied by fecundity.

To calculate the adjusted egg to emergence survival rate, we multiplied the spawning to

emergence survival rate, randomly generated using a normal distribution with a mean of 0.3 and standard deviation equal to 0.07 (Groot and Margolis 1991, modified by Bradford et al. 2000), by a density dependent adjustment factor regulated by the number of spawners present. That relationship is theoretically controlled by limited spawning area. When spawners were at equilibrium carrying capacity, there was no density dependent effect. Otherwise, the effect was described by a modified Richards 3-parameter model where incubation survival was gradually adjusted downward as spawners exceeded the equilibrium level or upward when spawners were less than equilibrium (Figure 3). Finally, we multiplied the adjusted egg to emergence survival rate by the potential number of eggs to generate the number of emerging fry.

The basic survival rate from emergence to smoltification was randomly generated using a normal distribution with a mean of 0.029 and standard deviation of 0.0029 (Groot and Margolis 1991, modified by Bradford et al. 2000). A density dependent pre-smolt survival adjustment factor was described by a modified Richards 3-parameter model, such that when the number of calculated fry was less than expected, the survival was gradually adjusted up to 2.0 times, but

when the calculated fry number was greater than expected, survival was adjusted downward to a minimum of 0.33 (Figure 4).

A nutrient-related pre-smolt survival adjustment factor was regulated according to the number of spawners relative to the equilibrium carrying capacity. A logistic equation described the relationship between the number of spawners and the nutrient input to the system (Figure 5). When the number of spawners was greater than the equilibrium carrying capacity, the survival rate was gradually adjusted upward to 2.0 times. When the number of spawners was less than or equal to the equilibrium carrying capacity, the nutrient adjustment had no effect on the emergence to smolt survival rate. The number of potential smolts was calculated by multiplying the emergence to smoltification survival rate by the density dependent adjustment and the nutrient adjustment.

Since coho salmon smolt production is apparently limited by available habitat (e.g., Nickelson 1998; Bradford et al. 2000), we compared the survival-based estimate of potential smolts to an estimate of the maximum expected smolts. The maximum smolt production was calculated from the user-input maximum smolts per 100 m² from which the model randomly gen-

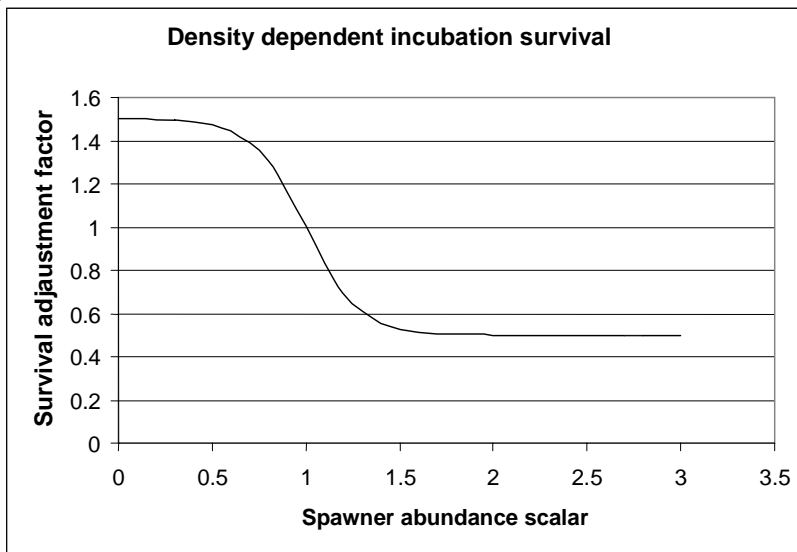


FIGURE 3. The incubation survival adjustment factor is set so that there is no effect when spawners are at the equilibrium carrying capacity. Incubation survival is adjusted according to the factor on the y-axis: reduced gradually to 50% as spawners increase above equilibrium or increased gradually to a maximum of 125% when spawners are less than equilibrium.

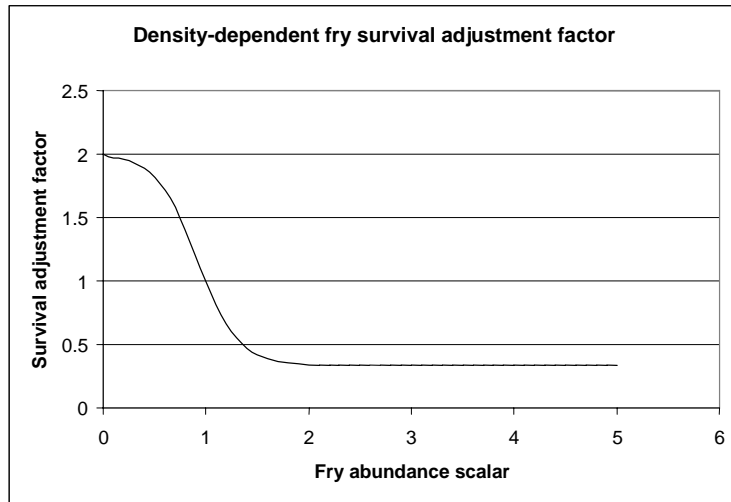


FIGURE 4. The fry density-dependent survival adjustment factor was 1 (no effect) when fry densities were equal to the maximum expected fry carrying capacity. When fry exceeded that point, the adjustment factor reduced fry survival down to 33%. When fry were less than the expected carrying capacity, survival was increased up to 2X.

erated a normal distribution of expected maximum smolts per area. The maximum number of smolts per area was then multiplied by the user-input available stream rearing area. The results were used as an upper cap on smolt production

if the survival-based estimate exceeded this area-based maximum smolt production.

The basic marine survival rate was randomly generated using a normal distribution with a mean of 0.05, standard deviation equal to 0.01 (Groot and Margolis 1991; Coronado and Hilborn

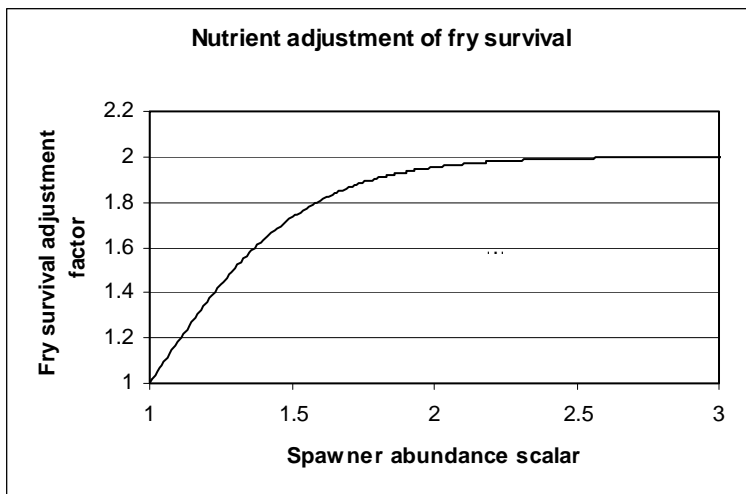


FIGURE 5. The nutrient-related fry survival adjustment factor: when the number of spawners was greater than the equilibrium carrying capacity, fry survival was increased up to 2.0 times; when the number of spawners was less than or equal to the equilibrium carrying capacity, the nutrient adjustment had no effect on the emergence to smolt survival rate.

1998). The marine survival rate was then adjusted by the nutrient-mediated growth factor, which was described by a logistic equation controlled by the number of spawners (Figure 6). When the number of spawners was less than or equal to the equilibrium carrying capacity, there was no adjustment to the marine survival rate. When the number of spawners was greater than the equilibrium carrying capacity the marine survival rate was adjusted by up to 1.75 times.

The overall effect of climate and environmental variability was incorporated with an adjustment factor that was based on a sine function having a randomly generated period ranging between 10 and 20 years, with a mean of 15 years (to approximately mimic patterns described by Beamish and Boullion (1993) and Hare et al. (1999). The periodicity and starting point of the cycle were randomly recalculated for each model iteration. The amplitude of the cycle ranged from 0 to 2. Each annual value was also stochastically adjusted to mimic the variation that is observed on the decadal oscillation (Figure 7). The climatic factor was then used to adjust coho salmon marine survival up or down. Marine survival rates were ultimately constrained so that they were never less than 2% nor greater than 20%, realistic bounds as reported in many populations by Coronado and Hilborn (1998).

Total adult returns were then calculated by multiplying the number of smolts by the adjusted marine survival rate. The user-input harvest level was taken as a percentage of the total return. To simulate a basic harvest conservation strategy, when the total run was less than 20% of the equilibrium carrying capacity escapement, the harvest rate was zero. If the run size was greater than 20% of equilibrium, the specified harvest rate was applied to the entire run.

The escapement was the difference between the total return and the harvest. Escapements completed the life cycle and were fed back into the next generation in the model. To help evaluate population performance, a nutrient factor was calculated by multiplying the two nutrient adjustments. The number of spawners relative to the carrying capacity regulated this factor.

Trials

We modeled the population 100 years into the future to observe performance under various scenarios. We used 100 iterations to dampen the sometimes extreme variation within individual model runs and to explore the “average” effects of the various density dependent and nutrient feedback loops. For this paper, we explored the effects of five different harvest rates (100 itera-

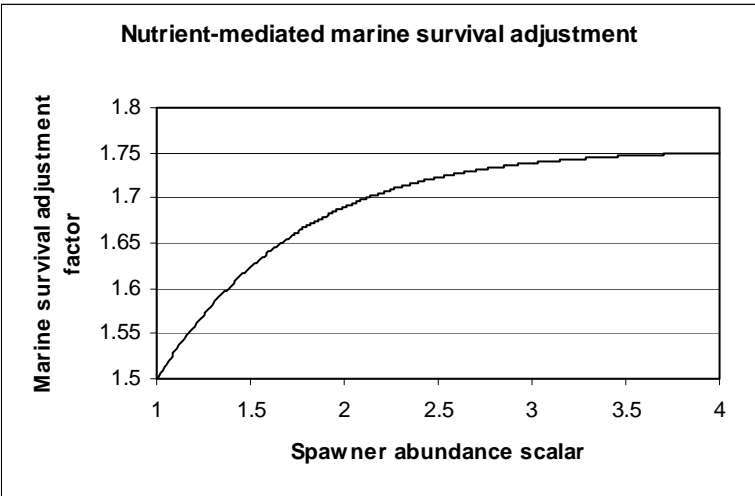


FIGURE 6. The nutrient-mediated marine survival adjustment increased survival gradually up to 1.75 times, as the number of spawners increased above the equilibrium carrying capacity. If the number of spawners was less than or equal to the equilibrium carrying capacity, there was no adjustment to the marine survival rate.

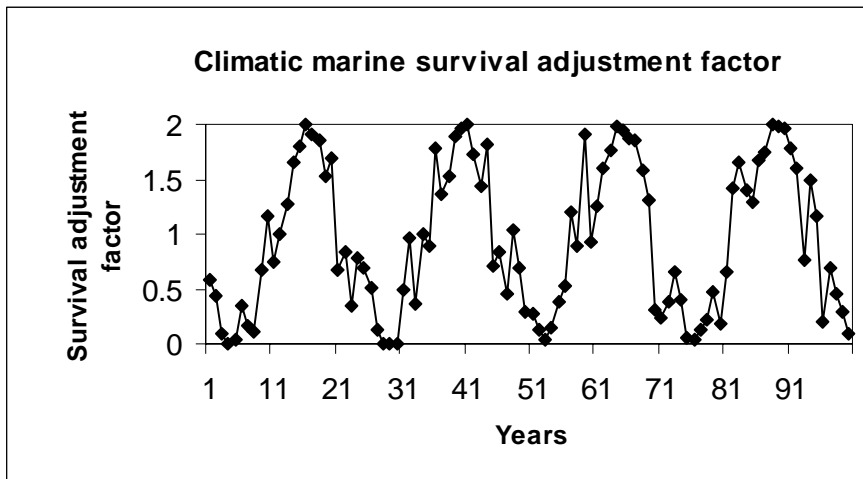


FIGURE 7. An example of the stochastically varied, decadal-oscillating marine survival adjustment factor.

tions each) on total run size, harvest, escapement, and nutrients. We used the following values as user inputs:

Spawner carrying capacity	5,000
Smolts per 100m ²	100
Stream rearing area (m ²)	95,000
Maximum fry to smolt survival	0.05
Harvest rates	0, 0.2, 0.4, 0.6, 0.8

Results and Discussion

Model Performance

The model appears to provide reasonable patterns when all the iterations are averaged (Figure 8). Because the model was developed to first simulate the unexploited equilibrium replacement, the unexploited total run size maintains itself around the 5,000-spawner equilibrium carrying capacity identified a priori for the system (Figure 8, top panel). The slight, gradual decay in the total returns with no exploitation is likely an artifact of the interrelationship between the survival rates, nutrient feedback, and the marine environmental variation.

Total run size was diminished by exploitation rates of 40, 60, and 80%, but there was not much apparent effect of 20% harvest. The results indicate that harvest rates greater than 20% tend to reduce the population over the first 20 years and then impose a persistent and relatively con-

stant reduction in production (Figure 8). At first glance, this raised concerns that the model may be oversimplified. However, performance of individual model runs indicates that the various density dependent or nutrient-related survival and growth adjustments are operating as expected; they tend to rebuild the population, sometimes dramatically, after it has been reduced. For example, in years when egg to fry survival was reduced due to high spawner densities, fry to smolt survival was compensatorily increased because the number of emerging fry was less than average, but then the number of potential smolts and/or the marine survival rate (influenced by smolt size) were adjusted upward because of carcass-derived nutrient input. Many times the model produced adults far exceeding the equilibrium replacement, as expected, but harvest eventually drove the population back down after several generations.

The performance observed in our simulations is logically reminiscent of the ecological performance of a natural population. The model is intended to mimic nature. Keeping in mind that an unexploited population would have evolved numerous compensatory mechanisms to replace itself and to normally realize a productive "surplus" to hedge against ecological downturns and catastrophes (e.g., Moberg et al. 1997), we have included five conditions under which the population would expand, and some of those are quite generous depending on population levels. Without exploitation, the popula-

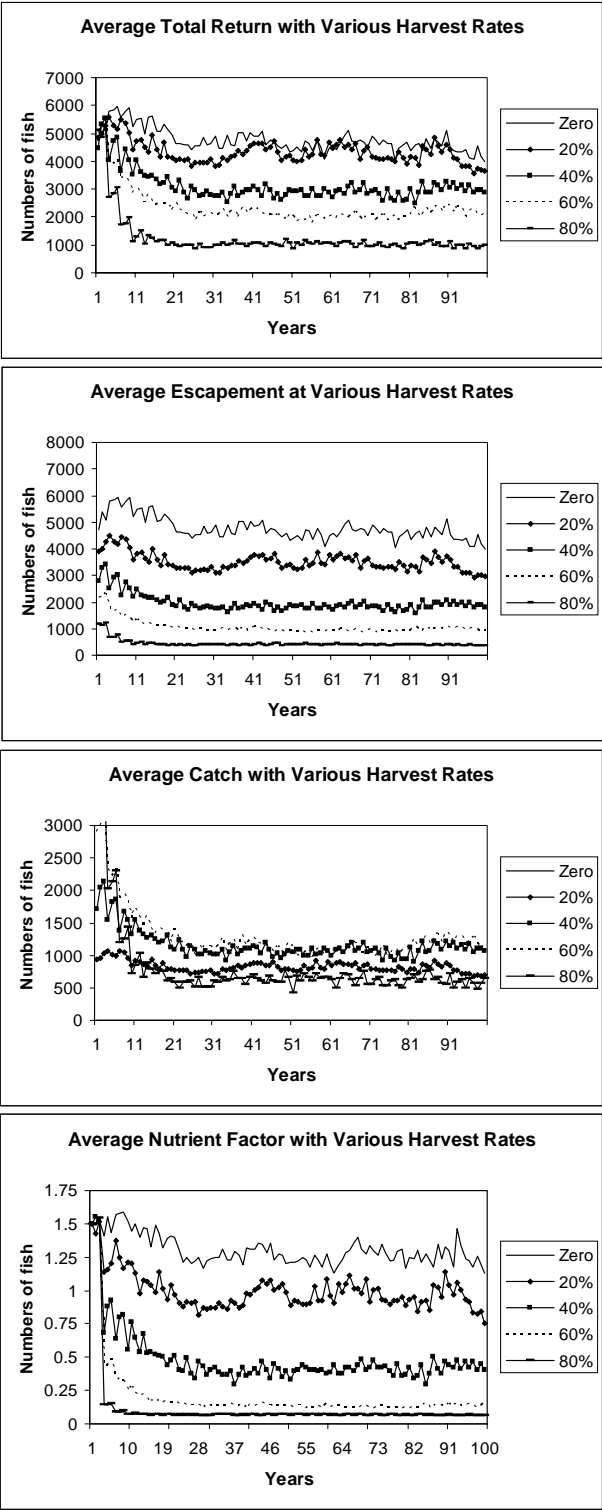


FIGURE 8. Model outcomes of an average of 100 iterations under 0, 20, 40, 60, and 80% harvest scenarios. Top panel, total run size; second panel, escapement; third panel, harvest; and bottom panel, nutrient factor.

tion maintained long-term equilibrium. The eventual reduction to a diminished steady replacement state under exploitation may indicate that a salmon population's innate production capacity can only rebuild the population over the short run, but that continued exploitation will, on average, depress the population according to the harvest rate.

Strengths and Weaknesses of the Model

We see four major benefits of this heuristic model. The first is that it provides an intuitive basis for thinking about how a salmon population functions. It therefore aligns management-oriented modeling with the animals' life history. In that sense, this life-history-based approach holds significant promise for restoration and sustainability because it accounts for most critical factors impinging on salmon population productivity. Previous work by Nickelson and Lawson (1998) followed this intuitive pathway, although they emphasized the viability of small populations rather than the sustainability of healthy populations.

Second, the modeling approach is exceedingly specific in its configuration of the life history and could conceivably include more terms than it does, thereby capturing most of the complexity and dynamics of salmon in their environment, as recommended by Mobrand et al. (1997). For example, we were able to reasonably incorporate several terms for the effects of marine-derived nutrients into our model. This approach is in sharp contrast to the highly generalized spawner-recruit models that are statistical expressions based on observed parental and resultant offspring run sizes. While statistical models must have few terms to accommodate the principle of parsimony (Hilborn and Liermann 1998), the life cycle approach is improved with additional terms.

Third, the model is organized in a clear, stepwise order that parallels the life history in a straightforward manner. Rather than depend on one primary mathematical or statistical expression, with a few terms added for influential variables, the model can incorporate as many steps as necessary, each having its literature-based biological function, with stochasticity as appropriate. While our approach is very similar to that of Nickelson and Lawson (1998), the use of a spreadsheet rather than computer coding makes

our model very accessible and understandable to a wide audience of potential users.

Fourth, this model allows examination and evaluation of various management scenarios. Once the model has been acceptably stabilized and appears to simulate the species and population of concern, it can be used to test the population's sensitivity to alterations in climate, nutrient inputs, harvest, or other relevant factors.

We recognize three drawbacks of our model. First, this model is very preliminary. Thus far, the model is theoretical and completely hypothetical, although based on realistic assumptions as well as means and standard deviations from the extensive available literature. Progress will require applying the concepts to some empirical case studies. We also recognize the need for incorporating an evaluation of uncertainty and risk associated with sensitivity analysis for management scenarios. Future refinement should include formal meta analysis to both build on previous knowledge and incorporate variation and uncertainty (Hilborn and Liermann 1998). Additionally, the spreadsheet model needs to be mathematically formalized as described by Prager and Mohr (2001).

Second, the model as configured uses 100 iterations to simulate the "average" outcome of the population, based on our estimated input parameters. In a practical application to a given population, many of the variables would be better known for that particular population. The model would then be used to assess how the population performs under a range of possible scenarios. This model is a generalization of real populations because it is based on 100 iterations of individual runs. The averaged iterations obscure the variation among individual model runs. Examination of individual model runs indicates a relatively wide range of outcomes. We caution that each natural population has only one outcome per generation and that outcome depends on the actual conditions experienced. However, once the model is based on empirical data, as recommended below, it should be useful in evaluating various projected outcomes for a given population. As an example, Nickelson and Lawson (1998) based their similar model on habitat quality in three specific coho-producing basins, an important step necessary for further development of our model.

Third, we realize our assumption of steady state conditions does not offer any new solutions to the problem of predictability. For example,

advances using traditional statistical approaches are gradually revealing some of the important environmental factors driving salmon marine survival, such as sea surface temperatures and upwelling (e.g., Hare et al. 1999; Pyper and Peterman 1999). While concepts based on the nature and extent of climatic changes and environmental variability have been incorporated into our model, they have yet to be cast in a predictive sense to account for future uncertainty. Likewise, direct links between environmental variation and survival have not yet been made in this model. On the other hand, specifying environmental fluctuation, as we have in this hypothetical situation, is like a natural experiment where the unknown environmental variation is controlled so that sensitivity to the effects of nutrients and harvest can be examined.

The Role of Nutrients in Escapement Management

We included a relatively simplistic accounting of the carcass-derived nutrient effects in this model. Nutrients had only positive effects; when escapement exceeded equilibrium carrying capacity, increased numbers of fry survived, they grew bigger and therefore survived better in the ocean. There were no imputed negative effects of reduced nutrients. Figure 8 (bottom panel) clearly indicates that the role of nutrients is diminished with harvest in this model, and we believe this may substantially explain the reduced population sustainability with increased exploitation.

We are unaware of any previous mechanistic models that have explicitly included the role of nutrients in the sustainability of salmon populations, although both Larkin and Slaney (1997) and Bilby et al. (2001) demonstrated the relationship between carcass-derived nutrients and salmon production. Nickelson and Lawson (1998), whose model was similar to ours and in some ways better developed, did not include specific consideration of nutrient feedback in their model. While no one has directly addressed the role of nutrients in escapement management directly, Stockner and MacIsaac (1996) and Bilby et al. (2001) recommend that nutrient enrichment should be accounted for in escapement management. Some important next steps for studying the role of nutrients using life history-based models include incorporating multi-year and multi-species effects of marine-derived nu-

trients and the effects of nutrients on estuarine productivity.

True Salmon Carrying Capacity

Accurately assessing true biological carrying capacity may be untenable but, we believe, a worthy goal to strive for. In a line of many previous attempts to estimate target production for coho salmon, Bradford et al. (2000) used the hockey stick model to estimate carrying capacity and escapement targets. However, their model, like their predecessors, was based on smolt production per female spawner and used contemporary data from exploited populations. It is possible that smolt production may be greater if watersheds were fully supplied with marine-derived nutrients and sufficient eggs resulted in enough fry to fully utilize the nutrient-enriched food base in the physical habitat. Furthermore, increased nutrients may result in larger smolts that apparently have better average survival than smaller smolts (e.g., Holtby et al. 1990).

For the present exercise, we assumed we knew true carrying capacity. Without empirical evidence, carrying capacity is difficult if not impossible to determine when the population is under exploitation. We suggest that one way to approach the estimation of carrying capacity is to use a model similar to ours, populated with empirical survival data, especially if those data are from populations that have been allowed to experience "overescapement" or nutrient enrichment, as well as a range of freshwater and marine survival conditions, and analyze the array of outcomes with various estimated equilibrium spawner numbers.

Salmon Escapement Management

Our life history-based model appears to provide some insight into why spawner-recruit models have not always resulted in thriving fisheries. First, we see no obvious evidence that salmon populations should consistently be expected to produce dramatic surpluses beyond their equilibrium capacity once they are under exploitation (a basic tenant of surplus production models, e.g., Ricker 1975). Even though our model includes many generous compensatory survival opportunities, the populations remained depressed under long-term exploitation. Generally, as the harvest rate increased, the model indicated

that continued exploitation brings the population to a "steady state" production level less than its inherent capacity (Figure 8). Interestingly, catch appeared to be maximized at 40–60% harvest, but 80% harvest resulted in the smallest catches (Figure 8, third panel). Although catch was greatest at 40–60% harvest in this model, the selection of alternative survival rates and nutrient feedback and environmental variation adjustments (i.e., a population with different compensatory capacity) would result in catch being maximized at a different harvest rate. Furthermore, at 40–60% harvest, the total run and escapement (Figure 8) are noticeably reduced, which may have important implications to the aquatic ecosystem and associated wildlife needs (Cederholm et al. 1999).

Second, if any of the data from model runs under exploitation were plotted with a standard spawner-recruit model, the conclusion would be that the population was in a "steady state" and the spawner-recruit model would result in an underestimate of the true equilibrium replacement point and an overestimate of the sustainable harvest rate.

In terms of direct application of this modeling approach to escapement management, several critical steps, described below, will be required before managers can use it to decide how many spawners should be allowed to escape the fishery to maximize productivity of a specific population. In the meantime, increasing evidence indicates that setting escapement goals at a fixed point based on traditional spawner-recruit models may result in underutilization of habitat capacity and may diminish nutrient supply (Cramer 2000). For example, Myers and Barrowman (1996) concluded that recruitment overfishing was pervasive but difficult to detect because so many populations were at low levels. Gilbert (1997) used similar analyses to conclude that spawner-recruit derivations of harvest and escapement reference points were valid for salmonids. Myers (1997) reanalyzed the same data and concluded that recruitment was indeed dependent on spawners. However, none of this work has differentiated the relative importance of spawners as delivery vectors of eggs into the gravel versus supplying nutrients for supporting future recruitment. Research by Bilby et al. (2001) provides a strong argument that allowance for nutrient replenishment in setting escapement goals will likely improve productivity. Cramer (2000) demonstrated that fishing at a level about

two-thirds less than that predicted through traditional spawner-recruit modeling could provide maximum harvests, while allowing the spawning stock to double. Until further research discerns the relative roles of spawners in delivering nutrients as well as eggs, and the amounts of each necessary for maximum production, the watchword should be generous escapements.

Recommendations

This model and other similar approaches (e.g., Nickelson and Lawson 1998) hold substantial promise for testing the sensitivity of salmon populations to a wide variety of both limiting and favorable factors that together influence population size. Custom configurations of this model should help to test effects like climate, catastrophic events, spawning population size, straying rates, hatchery supplementation, restoration alternatives, harvest scenarios, interspecific nutrient supplementation, or unique life history strategies on the various aspects of compensatory or depensatory survival. It can be used to study the population's resilience to perturbations, relative to various management options. With further refinement, the model can also interrelate multiple populations having unique survival rates but subject to the same fisheries or multiple fisheries with variable harvest rates.

Before this approach can be practically implemented, though, it must be evaluated relative to real, case history populations. As a first step, model performance should be evaluated by hind-casting run sizes for well-documented case history populations. This would require incorporating empirical survival data into the model from populations under exploitation but for which there is a long data record. To bring the model to its full utility, however, will require incorporating information on true carrying capacity. While there are no known, extant populations that are at unexploited equilibrium carrying capacity, it is essential that further research be conducted on equilibrium potential, rather than assuming that contemporary freshwater survival and productivity represent the population's potential. One way to do this is to stop fishing on some experimental populations having relatively unaltered habitat and observe production of smolts and adults as the population gradually resets itself to the suspected higher equilibrium point. An alternative approach to evaluating the model, as well as equilibrium

production, might include simulating smolt production and survival when carcass deposition reaches 0.15 kg/m², as suggested by Bilby et al. (2001).

Based on the outcomes observed in this model, taken in context with previous research, we make the following recommendations for Pacific salmon escapement research and management.

Research

- Continue modeling, as done here, testing various scenarios of harvest, survival, environmental variation, and other influences.
- Continue data collection on all aspects of survival, run sizes, smolt production, marine nutrient composition, and so on, for as many populations as possible, with an increased focus on marine and estuarine survival and production.
- Integrate this model with migration models and ocean condition models (e.g., Hinch et al. 1995).
- Conduct bioenergetic and feeding studies as they pertain to survival.
- Relate both physical habitat and nutrient enrichment to productive carrying capacity by
 - using historic records before harvest as compared with contemporary production,
 - evaluating contemporary nutrient contributions in a variety of streams having a range of escapements and harvest rates,
 - implementing intentional "overescapement" on several study streams to observe and understand true equilibrium replacement, and
 - continuing existing and establishing new, intensive study streams and expanding as necessary to assess production potential and capacity.
- Apply sensitivity analyses to life history population models to evaluate outcomes when environmental, nutrient, and survival rates are varied.
- Apply these and other related models to specific case study populations for which there is a rich data history (e.g., Puget Sound or Oregon coastal coho).

Management

- Ensure generous escapements (Larkin and Slaney 1997; NRC 1996; Bilby et al. 2001) by reducing or closing fisheries when necessary for long-term population health.
- Explore alternative methods of estimating escapement goals.
- Reduce direct reliance on spawner-recruit models—use only as one source of information in a precautionary approach that includes other considerations for sustainability, like those of Michael (1998), Cederholm et al. (1999), and Bilby et al. (2001).
- Consider replenishing nutrients to fresh waters where appropriate (Larkin and Slaney 1997; Stockner et al. 2000; Bilby et al. 2001).

Acknowledgements

We greatly appreciate quantitative assistance from Jeff Bromaghin. Nick Hughes provided spirited strategic consultation. The reviews of Jeff Bromaghin, Hal Michael, Jennifer Nielsen, Joel Reynolds, Carol Ann Woody, and several anonymous reviewers helped improve this manuscript.

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